

LATE QUATERNARY ANT FOSSILS FROM PACKRAT
MIDDENS (HYMENOPTERA: FORMICIDAE): IMPLICATIONS
FOR CLIMATIC CHANGE IN THE CHIHUAHUAN DESERT

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ABSTRACT

Packrat (*Neotoma* spp.) middens in rock-shelters provide important paleoecological records for the desert regions of North America. Specimens of various arthropod species accumulate in the middens and are cemented into a black, tarry mass by packrat urine.

We collected a variety of ants, including the genera *Labidus*, *Pseudomyrmex* (?), *Aphaenogaster*, *Crematogaster*, *Pheidole*, *Pogonomyrmex*, *Solenopsis*, *Trachymyrmex*, *Liometopum*, and *Camponotus* in packrat middens from the Chihuahuan Desert. Our data suggest a climatic change in the Chihuahuan Desert from mesic to arid during the past 45,000 years. The coniferous forest, oak-juniper woodland of the early Holocene changed to desert-grassland about 8250 radiocarbon years before present (yr BP), with a corresponding shift in ant species composition. By about 7500 yr BP, the presence of several arid adapted species suggests the establishment of desert environments. Finally after about 2500 yr BP, we see the occurrence of primarily desert adapted ant species in the Chihuahuan Desert, although mesic adapted species continue to occur in moist "islands" within the area. The paleoenvironmental data derived from the ant fossil records agrees closely with previous reconstructions based on other arthropods.

RESUMEN

FOSILES DE HORMIGAS EN NIDOS DE LAS RATAS
NEOTOMA: EVIDENCIA POR CAMBIOS DEL CLIMA EN EL
DESIERTO CHIHUAHUENSE – Nidos de la rata *Neotoma*

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ofrecen registros paleoecológicos de mucha importancia en las regiones áridas de Norte América. Ejemplares de varias especies de artrópodos se acumulan en los nidos y quedan cementados en una masa oscura formada con la orina de las ratas.

Colectamos una variedad de hormigas de varios géneros en nidos en el desierto chihuahuense en Estados Unidos y México. Nuestros datos sugieren que han habido cambios desde mésico hasta árido en los últimos 45.000 años. Bosques de coníferos, encinos y juníperos cambiaron a pastisales secos durante la primera parte del Holoceno (8.250 años antes del presente). Después hubieron varias especies adaptadas a los desiertos en los años 7.500 antes del presente. Finalmente observamos en forma predominante, la presencia de especies de hormigas adaptadas al desierto en los últimos 2.500 años, aunque quedan otras especies en "islas" mésicas del área. Los datos paleo-ambientales de hormigas están de acuerdo con datos de otros artrópodos.

INTRODUCTION

Packrat or woodrat (*Neotoma* spp.) middens are accumulations of objects including edible plants, cactus spines, insect remains, small pebbles and feces. These objects are carried to the den site for a variety of reasons, including food, protection and curiosity. In dry rock-shelters, these remains are cemented into black tarry masses by packrat urine and preserved for thousands of years, providing a rich paleoecological record for the Desert Southwest. This paper discusses fossil ants identified from ancient packrat middens from the Chihuahuan Desert. The midden localities, mostly in mountainous rock shelters and caves, form a northwest-southeast transect across this region (Fig. 1). The samples range in age from >43,300 yr BP to recent. Plant macrofossil analyses and radiocarbon chronologies have been published for these sites, as summarized by Van Devender (1990).

Elias (1987) made the first substantial report on midden insect assemblages from late Pleistocene and Holocene packrat middens in south-central New Mexico. Other insect fossil studies from packrat middens include sites in southwestern Arizona and northwestern Sonora, México (Hall *et al.*, 1988), and from the Ajo and Puerto Blanco mountains of Arizona (Hall *et al.*, 1989, 1990). Insect fossils (excluding ants) have also been analyzed from sites

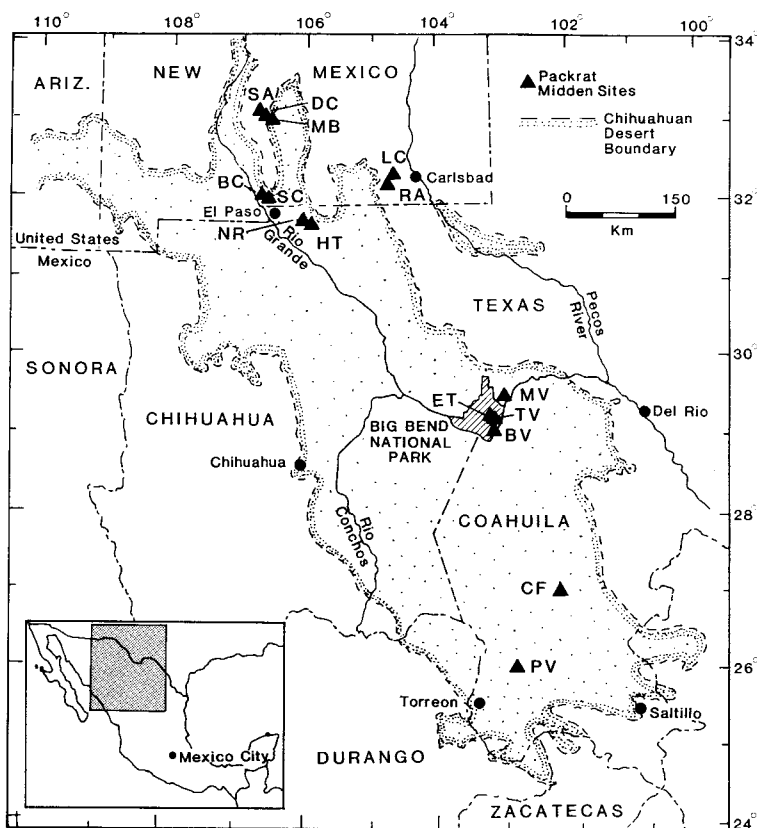


Figure 1. Map of the Chihuahuan Desert region, showing location of packrat midden sites from which ant fossils were identified. BC - Bishop's Cap, New Mexico; BV - Baby Vulture Den, Big Bend National Park, Texas; CF - Cañon de la Fragua, Coahuila, Mexico; DC - Dog Canyon, New Mexico; ET - Ernst Tinaja, Big Bend National Park, Texas; HT - Hueco Tanks State Park, Texas; LC - Last Chance Canyon, New Mexico; MB - Marble Canyon, New Mexico; MV - Maravillas Canyon Cave, Black Gap Wildlife Management Area, Texas; NR - Navar Ranch, Texas; PV - Puerto de Ventanillas, Coahuila, Mexico; RA - Rocky Arroyo, New Mexico; SA - San Andrés Mountains, New Mexico; SC - Shelter Cave, New Mexico; TV - Tunnel View site, Big Bend National Park, Texas.

reported in this paper (Elias and Van Devender, 1990, 1992; Elias *et al.*, 1992). The taphonomy of insect fossils found in ancient packrat middens has been discussed by Elias (1990).

We are unsure how the ants arrived at the middens. They appear to have been foragers and females ("queens") searching for a nesting site, as only a few individuals of a variety of species were found in any one midden. Some of the specimens could have been blown there. Most of the ants are probably too small to have been carried there by the woodrats. Middens are mesic habitats, with microhabitats more like mesic woodlands than arid deserts (Loring *et al.* 1987). Presumably ants would nest in such habitats, although nests have not been found in numerous excavated modern middens (Loring *et al.*, personal observation); large numbers of specimens of a single species are likewise not found in middens.

METHODS

Arthropod exoskeletal remains were sampled from 191 midden assemblages from 27 sites. Of these, 38 assemblages from 15 sites yielded ant fossils. For each assemblage, arthropod remains were sorted from wet-sieved midden matrix samples under a low-power stereo binocular microscope. Ant fossils were mounted on points for identification. The identifications were made using modern specimens for comparison. Most specimens were fragmented and many could not be identified to species. Voucher specimens are curated in the Laboratory for Environmental Biology, University of Texas, El Paso.

RESULTS

Nineteen species of ants were identified from the midden samples. The ant fossils were recovered from assemblages ranging in age from >40,000 yr BP to recent (Fig. 2). Six species were found in assemblages ranging in age from >40,000 to 10,000 yr BP (*Pheidole subdentata*, *Camponotus mina*, *C. festinatus*, *Aphaenogaster* nr. *texana*, *Liometopum luctuosum*, and *Pogonomyrmex barbatus*), five species were found in early to mid-Holocene age samples (*Aphaenogaster huachucana*, *A. albisetosa*, *Pogonomyrmex apache*, *P. desertorum*, and *P. texanus*), and three species were found only in samples younger than 1000 yr BP

Table 1. List of locations, ages, elevations and ant species found in Chihuahuan Desert middens.

Site	Location	Age (yr BP)	Elevation(m)	Species ¹
BC	Doña Ana Co., NM	10,650±170	1465m	Pb
BV	Brewster Co., TX	5560±120	670m	Cf, Casp, Cm, Pa, Pd, Pt, Phs
DC	Otero Co., NM	360±90	1615m	Anrt, Cf, Cm, Pssp
ET	Brewster Co., TX	15,160±440	760m	Casp
HT	El Paso Co., TX	9380±270	1420m	Ah, Anrt
		not dated	1420m	Cm
LC	Eddy Co., NM	10,010±160	1310m	Anrt
		7530±200/6770±300/1515±60	1310m	Aa
		10,010±160	1310m	Phs
		1515±60	1310m	Phsp
		3940±100	1310m	PW/PM-1, Phsp
		3940±100/850±90	1310m	Li
MB	Otero Co., NM	3300±110	1690m	Anrt, Pa
		2180±120	1690m	Phsp
MV	Brewster Co., TX	4680±160	610m	Anrt
		6020±110	610m	Pa, Posp
NR	Hudspeth Co., TX	9760±140	1340m	Cf
		6360±140	1340m	Aa
		9520±190/8320±200	1340m	Ah
		2550±120	1340m	Crsp
		9760±140	1340m	Pb

Table 1, Continued

Site	Location	Age (yr BP)	Elevation(m)	Species ¹
PV	Coahuila	560±80	1400m	Anrt, Cf, Crsp, Lc, Phs, Phsp, Sx, Tnrs
RA	Eddy Co., NM	230±80	1160m	Anrt
		230±80	1160m	Phs
		230±80	1160m	P.WPM-1
		230±80	1160m	Psp
		2940±190	1130m	Pa
SA	Otero Co., NM	10,590±400/9640±330	1585m	Ll
		10,590±400	1585m	P.WPM-1
SC	Doña Ana Co., NM	35,570±1100	1400m	Anrt
		>39,800	1400m	Cm
		>43,300	1400m	Phs
		>39,800	1400m	P.WPM-1
TV	Brewster Co., TX	15,540±650	760m	Casp
		1600±110	670m	Phs

¹ Species abbreviations: Aa, *Aphaenogaster albisetosa* Mayr; Ah, *Aphaenogaster huachuca* Creighton; Anrt, *Aphaenogaster* nr. *texana*; Cf, *Camponotus festinatus* (Buckley); Cm, *Camponotus minia* Forel; Casp, *Camponotus* sp.; Crsp, *Crematogaster* sp.; Lc, *Labidus coecus* (Latreille); Ll, *Liometopum luctuosum* Wheeler; Phs, *Pheidole subdentata* Pergande; Phsp, *Pheidole* spp. (apparently several species); Pa, *Pogonomymex apache* Wheeler; Pb, *Pogonomymex barbatus* (Smith); Pd, *Pogonomymex desertorum* Wheeler; Pt, *Pogonomymex texanus* Francke and Merickel; Posp, *Pogonomymex* sp.; P.WPM-1, undescribed *Pogonomymex* species (WPM-1); Pssp, *Pseudomymex* sp.; Sx, *Solenopsis xyloni* McCook; Tnrs, *Trachymymex* near *septentrionalis*.

primarily a subterranean predator with reduced nocturnal activity above ground.

One of our specimens appeared to be a male *Pseudomyrmex* of the subfamily Pseudomyrmecinae, but the specimen was poorly preserved and the identification is questionable.

We identified a variety of ants in the subfamily Myrmicinae, including the genera *Aphaenogaster*, *Crematogaster*, *Pheidole*, *Pogonomyrmex*, *Solenopsis*, and *Trachymyrmex*. *Aphaenogaster albisetosa* (Fig. 3, A) was found in Eddy Co. NM in deposits which were about 7500 years old. It is common today throughout the southwest USA and northern México in arid and semi-arid regions. It nests in the soil, usually in conjunction with large stones. It is omnivorous, but is also a predator. It is absent from extremely arid environments where *A. cockerelli* dominates. *Aphaenogaster* nr. *texana* (Fig. 3, B) is a member of the widely distributed and common *texana* species complex found throughout the southern USA and northern México. It appears to be most similar to *A. punctaticeps* MacKay, 1989, but differs in having a more elongate head and less developed propodeal spines. This species was widely distributed in the Chihuahuan Desert during the late Quaternary; it was found in midden samples as old as 35,000 yr BP from Eddy, Otero and Doña Ana Counties in New Mexico, and El Paso and Brewster Counties in Texas. This species was found in recent assemblages from Otero Co. New Mexico, and may still occur in the area. Species of this complex are occasionally found in arid regions, but are most common in mesic habitats including riparian environments and forests. *Aphaenogaster huachucana* (Fig. 3, C), another member of this species complex, is uncommon and is found today only in Colorado and southern Arizona. In the late Quaternary it was widely distributed in the Chihuahuan Desert, being found as far east as El Paso and Hudspeth Co. Texas about 10,000 years ago (Table 1).

We found identifiable fossil fragments of *Crematogaster* from two sites (BV and NR in Table 1). This is a common genus, found in a variety of different habitats. *Pheidole subdentata* (Fig. 3, D & E) was one of the common species, found in middens from six sites (BV, LC, PV, RA, SC, and TV in Table 1) occurring in the area from 230 to 43,000 years ago. This polymorphic species is not common in the United States (Arizona), but is very common in México, from the state of Chihuahua south to the interior. It is

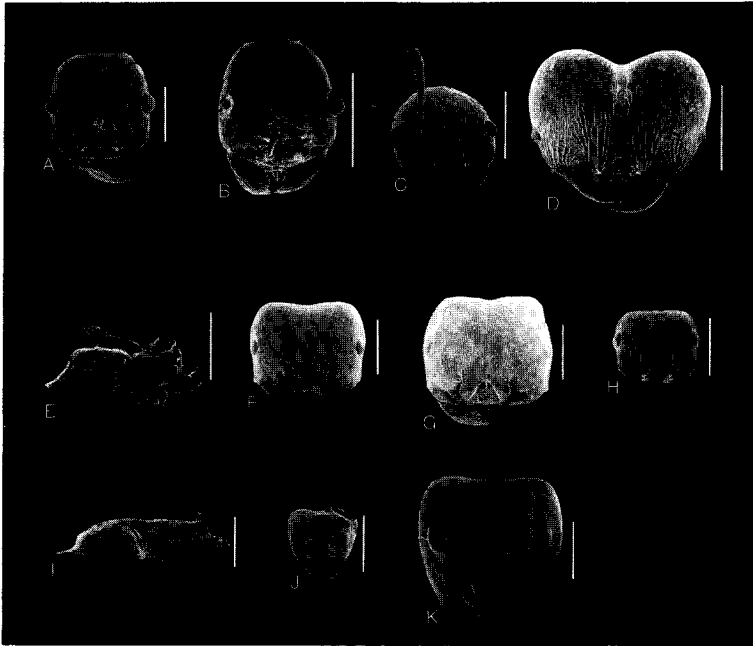


Figure 3. Scanning electron micrographs of fossil ant specimens from Chihuahuan Desert packrat middens. Scale bar equals 1 mm. A, head capsule of *Aphaenogaster albisetosa*; B, head capsule of *Aphaenogaster* nr. *texana*; C, head capsule of *Aphaenogaster huachucana*; D, head capsule of *Pheidole subdentata*; E, thorax of *P. subdentata*; F, head capsule of *Pogonomyrmex apache*; G, head capsule of *Pogonomyrmex barbatus*; H, head capsule of *Pogonomyrmex* species WPM-1; I, thorax of *P. species* WPM-1; J, head capsule of *Liometopum luctuosum*; K, head capsule of *Camponotus festinatus*.

most common in grasslands and sparse forests, nesting under rocks. We found several other *Pheidole* species, but these were impossible to identify as they were represented by fragments of workers.

The genus *Pogonomyrmex* was especially common in our samples. It is one of the most common ant genera throughout the southwestern USA and most of Mexico today. We found *P. apache* (Fig. 3, F) in middens from throughout its present day range, in assemblages spanning the last 6000 yr. It is found today from Nevada east to Kansas and south into Chihuahua, and we report it

here from Coahuila. *Pogonomyrmex texanus* is closely related to *P. apache* and is presently known only from western Texas and southern New Mexico. We found fossil specimens of this species in middens from Brewster Co. Texas (BV), in assemblages greater than 5000 years old. Both of these species are found in the Chihuahuan Desert today, where they nest in soil. Nests of these ants are difficult to find; they consist simply of an entrance hole with little or no surrounding soil (unusual in the genus) and colonies appear to be very small, probably on the order of a few hundred individuals (also unusual for the genus). *Pogonomyrmex barbatus* (Fig. 3, G) was also identified in samples from Doña Ana Co., NM and from Hudspeth Co. TX (Table 1). It occurred in the area for several thousand years. This species is widely distributed today in the southern USA south into most of Mexico. It is rarely found in arid habitats (in only urban and agricultural areas), but is very common in mesic habitats throughout its range. It is replaced by the equally common *P. rugosus* in arid habitats, a species which we did not find in the fossil assemblages. *Pogonomyrmex desertorum* is another species of this genus, which we found from one fossil site (BV); it occurred there more than 5000 years ago. It is especially common today in arid habitats in the Chihuahuan Desert. It is a small harvester ant that builds small mounds in the soil. We identified several other pieces of specimens of *Pogonomyrmex*, one of which may represent an undescribed species (WPM-1) (Fig. 3, H & I). This species is a member of the *barbatus* complex and is closely related to *P. barbatus* and *P. rugosus*, but differs in that the cephalic rugae diverge posteriorly and are somewhat more coarse. It is also smaller, but may simply be a minimum of another species. This species occurred in Eddy Co. and Otero Co. NM from 230–10,000 yr BP and is probably still present in the area.

The genus *Solenopsis* was rare in our samples; we found only the species *S. xyloni*. It is a common, widely distributed species in the southern USA and northern Mexico, and is one of the most common species in the Chihuahuan Desert today, with moderately large colonies nesting in the soil. We identified one worker of this species from a midden in Coahuila (Table 1); it occurred there about 500 years ago.

We found fossils of an undescribed species of *Trachymyrmex* nr. *septentrionalis* in midden assemblages from Coahuila (Table 1). It appears to be conspecific with an undescribed species of the genus which occurs today in Chihuahua. When it is found in deserts, this genus usually occurs in mesic habitat islands (i.e., arroyos, playa fringes, etc.). Ants of this genus nest in the soil and use desert vegetation, especially mesquite (*Prosopis* spp.) to raise fungus gardens. We did not find specimens of *T. smithi*, which is the most common extant southwestern desert species (Arizona, New Mexico, Texas, Chihuahua).

We found only a single representative of the Subfamily Dolichoderinae in our samples. *Liometopum luctuosum* (Fig. 3, J) was found in middens from Eddy Co. (RA) and Otero Co. (SA) New Mexico. This species nests in dead logs in pine forests at higher elevations (1200–2400 meters) in North America today. It is surprising that we did not find the more common species, *L. apiculatum*, which nests in the soil and logs throughout the Chihuahuan Desert and surrounding oak forests today.

The subfamily Formicinae was represented in the fossil assemblages only by the genus *Camponotus*. *Camponotus festinatus* (Fig. 3, K) is one of the most common desert *Camponotus* species. It nests in the soil under rocks. *Camponotus mina* is rarely collected, and nests in trees, especially mesquite. It was apparently more common regionally in the past. Our fossil records of *C. mina* extend the distribution from southern Arizona and northern Sonora to New Mexico and the Big Bend region of Texas (Table 1). We found additional pieces of *Camponotus* which could not be identified.

Our specimens suggest a much more mesic climate in the past. We collected specimens of many species which are presently found only in mesic habitats. For example, we found *Pogonomyrmex barbatus* instead of *P. rugosus*, which is a dominant species in arid regions today. Our *Pogonomyrmex* species belonged to the *barbatus* species complex, not to the *maricopa* complex, which is common in this region today. We also found the forest inhabiting *Liometopum luctuosum* instead of the desert adapted *L. apiculatum*. Many of the species we found in the fossil assemblages are rarely found today, and seem to be remnants of much larger populations in the past.

DISCUSSION

The late Quaternary paleobotanical record of the Chihuahuan Desert has been summarized by Van Devender (1990). The vegetation gradients of the Chihuahuan Desert reflect regional precipitation and temperature regimes, with desert-scrub communities in the hot, dry lowlands of the Big Bend of Texas (600–1675 m) and at the southern end of the desert in the Bolsón de Mapimí (1075–2000 m), gradually replaced by desert-grassland to the north, west, south and southeast. Pine-oak woodland and pine forest occur at higher elevations (montane islands) in the desert, and on the surrounding mountain ranges (Van Devender, 1986). The Bolsón de Mapimí vegetation reaches its northern limit in the Rio Grande lowlands (600–1070 m) from Big Bend National Park to northwest of Presidio, Texas. The desert in the Big Bend region is bounded by grasslands and oak woodlands of the Davis Mountains on the north, and by the Chisos Mountains on the south.

At the northern end of the desert, a pinyon-juniper-oak woodland dominated limestone slopes from 1270–1495 m in elevation during the middle to late Wisconsin interval (42,000 to 10,800 yr BP). Early Holocene oak-juniper woodland gave way to desert-grassland after about 8,250 yr BP. After about 4,200 yr BP, desert plant species migrated into the northern Chihuahuan Desert region, forming a relatively modern desert-scrub vegetation on rocky slopes. The fossil arthropod assemblages (mostly Coleoptera) from the northern region exhibit a series of species shifts indicative of substantial environmental change since the middle of the last glaciation (Elias, 1992). In full-glacial (22,000–18,000 yr BP) assemblages, the arthropod record suggests that coniferous woodland was widespread. Ant species adapted to mesic habitats were present in these areas, including *Liometopum luctuosum*, *Pogonomyrmex barbatus*, *Aphaenogaster* nr. *texana*, *A. huachucana*, *Camponotus mina* and *Pheidole subdentata*. From about 22,000 to 11,000 yr BP, woodland environments persisted, but the insect data suggest that there was considerable open ground, with grasses at least locally important. The transition from the Wisconsin-age temperate fauna to the more xeric fauna of the post glacial interval started at about 12,500 yr BP, with the arrival of the first xeric-adapted species. By about 7500 yr BP, the appearance of additional xerophilous species indicates the establishment of desert

environments, including desert grasslands. During this time mesic adapted ant species were replaced by arid adapted species, including *Pogonomyrmex* spp. and *Pheidole* spp. After 2500 yr BP, the last of the temperate ant species were replaced by species associated with desert-scrub communities, including such species as *Pogonomyrmex desertorum* and *P. apache*.

In the Big Bend region, the insect assemblages suggest greater effective moisture during the late Wisconsin interval (ca. 30,000 to 12,000 yr BP), with an especially diverse, mesic fauna during the earlier part of this interval. Ant species present at that time included *Camponotus* spp. By latest Wisconsin times, many grassland species occurred in the Big Bend region that are now confined to cooler, moister regions to the north and to higher elevations. After 12,000 yr BP, most of these temperate grassland species are replaced by either desert species (*Pogonomyrmex desertorum*, *Camponotus festinatus*) or by more cosmopolitan taxa that are known today from both desert and grassland (*Pogonomyrmex apache*, *P. texanus*, *Pheidole subdentata*). This change suggests a climatic shift from cool, moist conditions of Wisconsin glacial times to hotter, drier conditions of latest Wisconsin and early Holocene time. In Big Bend, the insect species indicative of more severe aridity are first recorded at about 6000 yr BP, with some relatively temperate species persisting until about 2500 yr BP. Mesic species are still found in the area in mesic "islands" (Van Pelt, 1983; MacKay and Anderson, 1991).

In the Bolsón de Mapimí, paleobotanical analyses show that the late Wisconsin vegetation on the limestone slopes was a woodland dominated by junipers (*Juniperus* sp.) and papershell pinyon (*Pinus remota*) in association with succulents. The abundance of papershell pinyon declined from 13,120 to 12,380 yr BP as succulents increased. The late glacial insect assemblages, ranging in age from 13,590 to 12,280 yr BP, comprise a mixture of temperate and desert taxa (Elias et al., 1992). However, most of the desert-associated species are phytophages, and their presence in the fossil assemblages is more indicative of certain desert floristic elements than of xeric climate *per se*. Several of the beetle species identified from late glacial assemblages have tropical to subtropical affinities. There is a temporal hiatus in the midden samples from 12,000 to 9000 yr BP, after which most of the late glacial insect species

disappear from the records. Beetles associated with desert-scrub communities dominate in the early and middle Holocene assemblages. In the late Holocene, several different insect species are recorded, including both temperate species and desert species. Both the paleobotanical and arthropod records from the Bolsón de Mapimí indicate that this region served as a refugium for desert biota during the late Pleistocene. The southerly latitude of this region appears to have dampened the climatic effects of the Wisconsin glaciation to the extent that desert species could survive there, at least during the late glacial interval but also presumably prior to this. A mosaic of temperate and xeric habitat has been available to the regional biota, even during the last 1000 yr, when other regions of the Chihuahuan Desert have experienced extremes of aridity (Elias and Van Devender, 1990, 1992). The only Mexican midden sample that yielded ant fossils (the PV site in Coahuila) was dated to the late Holocene arid interval. It contained several species of ants (Table 1), including desert, grassland, and tropical species, all of which live in Mexico today.

The paleoenvironmental conditions inferred from the fossil ant data agree quite well with paleoenvironmental reconstructions based on other fossil arthropods (mostly beetles). While this degree of harmony is gratifying, it is not unexpected. Most of the ant species found in our samples are detritivores or predators, and are therefore not tied to specific types of vegetation. Detritivores and predators are more common in desert insect communities than in the temperate zone (Crawford, 1988); these are useful adaptations in regions of scarce food resources. Many of the beetle species found in the fossil midden samples (e.g., in the families Carabidae and Tenebrionidae) are detritivores or predators.

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